

## **SPIDERS (ARANEAE) ASSOCIATED WITH STRIP-CLEARCUT AND DENSE SPRUCE-FIR FORESTS OF MAINE<sup>1</sup>**

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### **ABSTRACT**

Spiders of 15 families, 76 genera, and at least 125 species were collected by pitfall traps in a spruce-budworm infested forest of northern Maine. Species of Lycosidae were numerically dominant and accounted for 56.2 and 54.1% of the total trapped specimens in 1977 and 1978, respectively. For both study years, significantly more ( $P \leq 0.05$ ) individuals and species of spiders were captured in clearcut strips than in either uncut residual strips or dense stands. Peaks in seasonal activity of spiders generally coincided with the spruce budworm's early and late larval stages; spiders were also abundant and active during budworm oviposition and dispersal of 1st instars. Diversity of spider species was generally greater in dense stands and uncut residual strips than in clearcut strips. Individuals were distributed unevenly among species but more evenly in dense stands and uncut residual strips than in clearcut strips. Coefficients of community (CC) and percentage similarity (PS) values indicated more spider species than individuals were shared in common among forest conditions. Neither age of strip clearcut (1-6 years) nor litter depth had much influence on mean catches and mean numbers of species of spiders per trap per week.

### **INTRODUCTION**

Spiders are among the dominant predators in many terrestrial communities (Gertsch 1979). In northeastern spruce-fir forests, arboreal spider densities are estimated to range from 187,500/ha (Morris 1963) to 312,500/ha (Haynes and

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Sisojevic 1966). These estimates do not include the epigeal and terricolous faunas that live near the ground. And, despite their common occurrence and potential importance as predators of insect pests (Riechert 1974), little is known about the species composition, diversity, and abundance of spiders that inhabit individual forest stands, forest-stand types, or forest communities in North America. Some earlier studies of forest-spider faunas include those of Dowdy (1950), Elliott (1930), Gibson (1947), Stratton et al. (1979), and Uetz (1979).

The possible adverse or beneficial effects of forest management practices on spider populations also have received scant attention, particularly in North America. Coyle (1981) studied the effects of clearcutting on the spider community of a southern Appalachian forest in North Carolina. The effects of silvicultural practices on European forest spiders have received more attention; studies include those by Huhta et al. (1967, 1969) and Huhta (1971).

As part of our investigations on natural enemies of the spruce budworm, *Choristoneura fumiferana* (Clem.), we studied the spider fauna of strip-clearcut and dense (uncut) spruce-fir forests of northern Maine in 1977 and 1978. Spruce budworms are susceptible to ground-inhabiting predators when 1st and 2nd instars disperse (Mott 1963; Jennings et al. 1983), and when large larvae and pupae drop from host-tree crowns to the forest floor (Morris and Mott 1963; Kelly and Régnière 1985). Our objectives were to: (1) determine the species of ground-inhabiting spiders in uncut residual strips, clearcut strips, and dense (uncut) spruce-fir stands, (2) determine seasonal activities of ground-inhabiting spiders as they relate to spruce budworm development, and (3) determine possible effects of strip clearcutting on species diversity and evenness of distribution of spiders. We also investigated effects of strip-clearcut age and litter depth on numbers and species of spiders.

## MATERIALS AND METHODS

**Study area.**—We studied spiders in a dense spruce-fir forest infested with spruce budworm. Portions of the forest had been strip clearcut by mechanical harvesters; this created open strip areas with abundant shrubs and forbs, mainly *Rubus* spp. Strip clearcutting resulted in alternating clearcut and uncut residual strips (Fig. 1). Individual study sites were located from 48 to 61 km northwest of Millinocket, Piscataquis County, Maine, between Telos and Harrington Lakes (45° 45' to 46° 10' N, 68° 55' to 69° 20' W). Elevations ranged from about 360 to 425 m. The forest stands previously had been infested with spruce budworm for 4 to 5 years. The study area was sprayed with Sevin-4-oil® for spruce budworm suppression in 1976, but was not sprayed in 1977 or 1978. Budworm population estimates were 92.8 larvae-pupae/m<sup>2</sup> of balsam-fir foliage in 1977, and 100.7 larvae-pupae/m<sup>2</sup> of foliage in 1978.

Five strip-clearcut stands and five nearby dense (uncut) stands were investigated in 1977; seven strip-clearcut stands and three dense stands were investigated in 1978. In 1978, three each of the strip-clearcut and dense stands were the same as those studied in 1977; four additional strip-clearcut stands were investigated to obtain information on possible effects of strip-clearcut age on spider populations. Strip widths ranged from 23.4 to 49.7 m for uncut residual

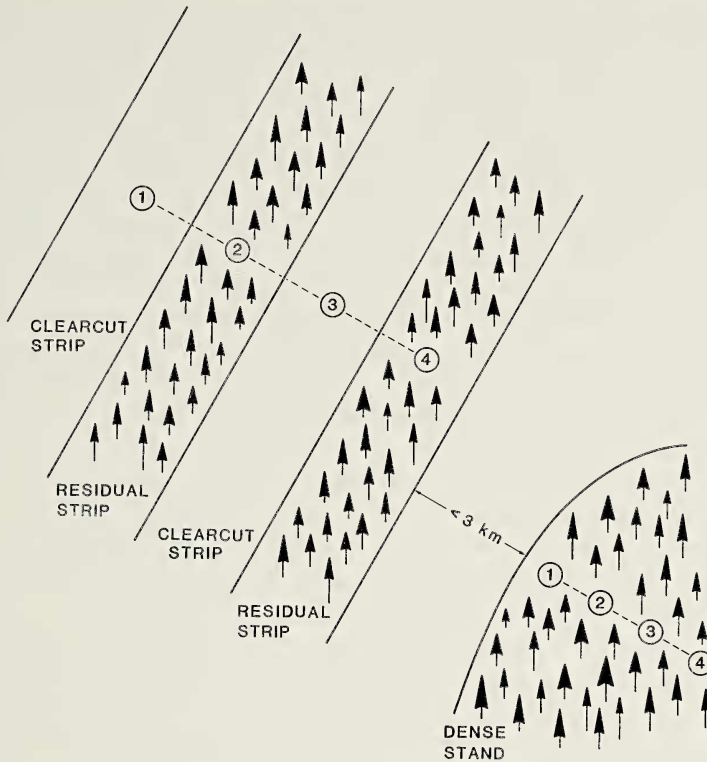


Fig. 1.—Pitfall-trap layout in strip-clearcut (uncut residual and clearcut strips) and in nearby dense (uncut) spruce-fir stands, Piscataquis County, Maine.

strips and from 19.1 to 29.7 m for clearcut strips investigated in 1977. Strip widths were not measured in 1978 but were comparable to those studied in 1977.

Mean basal areas, tree heights, and stand ages in 1977 were: 33.1 m<sup>2</sup>/ha, 17.3 m, and 73.7 years for uncut residual strips; 41.5 m<sup>2</sup>/ha, 15.4 m, and 73.5 years for dense stands. Most study sites had a predominantly softwood component of balsam fir, *Abies balsamea* (L.) Mill.; red spruce, *Picea rubens* Sargent; white spruce, *P. glauca* (Moench) Voss; black spruce, *P. mariana* (Miller) B.S.P.; northern white cedar, *Thuja occidentalis* L.; and white pine, *Pinus strobus* L. Common hardwood species were paper birch, *Betula papyrifera* Marshall; yellow birch, *B. alleghaniensis* Britton; and red maple, *Acer rubrum* L. Species composition by percentage basal area indicated that dense stands had more spruce (80%) than fir (11%), whereas spruce (45%) and fir (43%) were about equally represented in the uncut residual strips studied in 1977. The additional uncut residual strips studied in 1978 had more spruce (61%) than fir (30%). Hardwood basal area percentages generally were < 5% for both dense stands and uncut residual strips.

Understory vegetation differed markedly among the forest conditions. The open cleared strips had an abundance of flowering shrubs and forbs such as *Kalmia angustifolia* L., *Prunus pensylvanica* L., *Vaccinium angustifolium* Aiton, and *Rubus* spp. The uncut residual strips and dense stands, on the other hand, were characterized by few, widely spaced or clumped plants such as *Maianthemum canadense* Desfontaines, *Oxalis montana* Rafinesque-Schmaltz, and *Cornus canadensis* L. No quantitative plant data were taken; however, plants of 21



families, 43 genera, and at least 50 species were collected and identified (Jennings and Houseweart, unpublished data). Most plant species were collected in open areas of strip clearcuts; only five species were collected in uncut residual strips and 10 species in dense (uncut) stands.

**Pitfall traps.**—Forty large-capacity pitfall traps (Houseweart et al. 1979) were used each year for collecting spiders. Although pitfall catches are biased toward active forms, pitfall trapping remains the best available means for sampling wandering spiders (Uetz 1975), and trap catches give a closer estimate of species diversity than quadrat sampling (Uetz and Unzicker 1976). Our large-capacity trap (1 liter) had a 30-cm<sup>2</sup> apron with a 14.9-cm-diameter hole for funnel-bottle suspension. Cutler et al. (1975) showed that traps with aprons caught twice as many dionychous spiders compared to traps without aprons. We added ca. 300 ml of a 1:1 mixture of ethylene glycol and 70% ethanol to each trap bottle as a killing-preserved agent.

Four traps were placed in each strip-clearcut area, one each in two cut strips and in two adjacent uncut residual strips (Fig. 1). Correspondingly, four traps were placed in each nearby dense (uncut) stand investigated. Trap spacings in strip clearcuts were duplicated in dense stands. Traps were installed on 26 May and their contents collected weekly thereafter for 10 weeks from 2 June to 4 August 1977. In 1978, traps were installed on 18 May and contents collected weekly thereafter for 11 weeks from 25 May to 3 August. For both study years, trapping periods corresponded with spruce budworm activity, i.e., larval feeding in May and June; pupation in late June; moth emergence, mating, and egg laying in mid July (Houseweart et al. 1982); and dispersal of 1st instars in late July (Jennings et al. 1983).

Trap contents were sorted in the laboratory; all spiders were removed and stored in 2-dram neoprene-stoppered vials containing 70% ethanol. Species determinations were made chiefly after Kaston (1981). Other consulted sources included: Opell and Beatty (1976) for the hahniids; Leech (1972) for the amaurobiids; Chamberlin and Gertsch (1958) for the dictynids; Levi (1957) for species of *Theridion*; Dondale and Redner (1982) for the clubionids; Dondale and Redner (1978) for the philodromids and thomisids; and Kaston (1973) for species of *Metaphidippus*. Numerous taxonomic papers were consulted for identification of the erigonids; most were identified by comparison with published species descriptions and with voucher specimens housed in the Canadian National Collection, Ottawa. A few adult erigonids could not be determined to species and were designated as sp. 1, sp. 2, etc.

Because most species descriptions are based chiefly on the genitalia, only sexually mature spiders were identified to species. Juvenile and penultimate stages were identified to generic level; recently emerged spiderlings to family level. A few badly damaged specimens were undeterminable. Representative specimens of most collected spider species are deposited in the arachnid collections of the American Museum of Natural History, New York; the Canadian National Collections of Insects, Arachnids, and Nematodes, Ottawa; and, the U.S. National Museum of Natural History, Washington.

**Litter depth.**—Because litter structure and depth significantly affect abundances of some forest floor spiders (Uetz 1979; Bultman et al. 1982), we measured litter depth (cm) near each pitfall trap ( $n = 40$ ). Measurements were summed and



means calculated over all replications by forest stand condition (uncut residual strip, clearcut strip, dense stand).

**Data analysis.**—Pitfall-catch data were subjected to Hartley's Test for homogeneity of variance prior to statistical analyses. Natural log transformations,  $\ln(X + 1)$ , were used to stabilize variances. Analysis of variance (ANOVA) and Duncan's Multiple Range Test were used to evaluate differences in pitfall catches over all weeks among the three forest stand conditions (uncut residual strips, clearcut strips, and dense stands) at  $P \leq 0.05$ . Regression analyses were used to evaluate the effects of strip-clearcut age (1-6 yr) and litter depth (independent variables) on mean catches of both individuals and species (dependent variables) per trap per week, where  $R^2$  = coefficient of determination.

Because our pitfall collections represented finite populations where all captured individuals were counted and identified (Pielou 1966; Poole 1974), we used Brillouin's diversity formula to calculate species diversity. The formula as defined by Pielou (1975 p. 10) is:  $H = 1/N \log N! / \prod N_i!$  where  $N$  is the number of individuals in the whole collection (i.e., for each forest condition) and  $N_i$  is the number in the  $i$ th species for  $i = 1, \dots, s$ . Brillouin's formula has been used to compare pitfall-catch diversities of spiders (Doane and Dondale 1979), carabid beetles (Reeves et al. 1983), phalangids (Jennings et al. 1984), and ants (Jennings et al. 1986). A measure of evenness was determined by the formula  $J = H/H_{\max}$  where  $H$  is Brillouin's diversity and  $H_{\max}$  is the maximum possible diversity. Two measures of similarity among forest conditions were made using coefficient of community (CC) and percent similarity (PS) (Pielou 1975), where (CC) measures similarity between species lists and (PS) measures similarity between species quantities.

## RESULTS

**Numbers of individuals and species.**—Fully 11,107 spiders, representing 15 families, 76 genera, and at least 125 species were collected by pitfall traps in spruce-fir forests of northern Maine. Fifteen families, 62 genera, and at least 97 species were trapped in 1977; 15 families, 66 genera, and at least 105 species were trapped in 1978 (Table 1). Generic and species composition differed between years. Ten species were captured in 1977 but not in 1978; 14 species were trapped in 1978 but not in 1977. For both years of trapping, individuals of Lycosidae were numerically dominant, comprising 56.2 and 54.1% of the total specimens trapped in 1977 and 1978, respectively. The Erigonidae, Amaurobiidae, and Agelenidae were next in abundance; each of the remaining families accounted for less than 10% of the total spiders caught either year.

Although the 40 pitfall traps were distributed unevenly among forest conditions, for both study years more spiders were captured in the clearcut strips than in either the uncut residual strips or in the dense spruce-fir stands. By far the majority of spiders caught in the open, cleared strips were species of *Pardosa* and undetermined lycosid spiderlings. Members of no other genus or family approached the abundance of wolf spiders in clearcut strips.

For both study years, about equal numbers of spider species were collected in dense, uncut spruce-fir stands (Table 1). In 1978, more species of spiders were caught in clearcut strips than the other two forest conditions.

Table 1.—Species and numbers of spiders collected in pitfall traps, three forest conditions, Telos Lake area, Piscataquis County, Maine, 1977-1978 (C = clearcut strips; R = uncut residual strips; D = dense stands; N = number of pitfall traps)

| Spider Species                  | 1977             |                  |                  |       |      | 1978             |                  |                  |       |      |
|---------------------------------|------------------|------------------|------------------|-------|------|------------------|------------------|------------------|-------|------|
|                                 | C                | R                | D                | Total | %    | C                | R                | D                | Total | %    |
|                                 | Strips<br>(N=10) | Strips<br>(N=10) | Stands<br>(N=20) |       |      | Strips<br>(N=14) | Strips<br>(N=14) | Stands<br>(N=12) |       |      |
| AGELENIDAE                      |                  |                  |                  |       |      |                  |                  |                  |       |      |
| <i>Agelenopsis utahana</i>      | 1                | 3                | 4                | 8     | 0.20 | 22               | 23               | 11               | 56    | 0.79 |
| <i>Agelenopsis</i> sp.          | 0                | 0                | 1                | 1     | 0.02 | 3                | 1                | 0                | 4     | 0.06 |
| <i>Cicurina brevis</i>          | 7                | 9                | 17               | 33    | 0.83 | 10               | 26               | 24               | 60    | 0.85 |
| <i>Cicurina pallida</i>         | 4                | 8                | 14               | 26    | 0.65 | 15               | 13               | 5                | 33    | 0.47 |
| <i>Cicurina placida</i>         | 0                | 0                | 1                | 1     | 0.02 | 0                | 0                | 0                | 0     |      |
| <i>Cicurina</i> sp.             | 4                | 2                | 4                | 10    | 0.25 | 10               | 3                | 1                | 14    | 0.20 |
| <i>Coras montanus</i>           | 0                | 0                | 4                | 4     | 0.10 | 1                | 1                | 1                | 3     | 0.04 |
| <i>Coras</i> sp.                | 0                | 1                | 1                | 2     | 0.05 | 0                | 0                | 0                | 0     |      |
| <i>Cryphoea montana</i>         | 1                | 12               | 19               | 32    | 0.80 | 6                | 85               | 51               | 142   | 2.00 |
| <i>Cryphoea</i> sp.             | 0                | 0                | 2                | 2     | 0.05 | 0                | 1                | 0                | 1     | 0.01 |
| <i>Wadotes calcaratus</i>       | 5                | 43               | 105              | 153   | 3.81 | 33               | 121              | 102              | 256   | 3.61 |
| <i>Wadotes</i> sp.              | 2                | 5                | 9                | 16    | 0.40 | 8                | 22               | 17               | 47    | 0.67 |
| HAHNIIDAE                       |                  |                  |                  |       |      |                  |                  |                  |       |      |
| <i>Antistea brunnea</i>         | 1                | 0                | 1                | 2     | 0.05 | 0                | 0                | 1                | 1     | 0.01 |
| <i>Hahnia cinerea</i>           | 0                | 0                | 5                | 5     | 0.12 | 2                | 0                | 2                | 4     | 0.06 |
| <i>Hahnia</i> sp.               | 0                | 0                | 1                | 1     | 0.02 | 0                | 0                | 0                | 0     |      |
| <i>Neoantistea agilis</i>       | 0                | 0                | 0                | 0     |      | 3                | 0                | 1                | 4     | 0.06 |
| <i>Neoantistea magna</i>        | 69               | 14               | 16               | 99    | 2.46 | 256              | 65               | 33               | 354   | 5.00 |
| <i>Neoantistea</i> sp.          | 8                | 0                | 1                | 9     | 0.22 | 52               | 1                | 2                | 55    | 0.78 |
| Undet. sp.                      | 1                | 0                | 2                | 3     | 0.08 | 1                | 0                | 0                | 1     | 0.01 |
| AMAUROBIIDAE                    |                  |                  |                  |       |      |                  |                  |                  |       |      |
| <i>Amaurobius borealis</i>      | 8                | 42               | 134              | 184   | 4.58 | 33               | 42               | 18               | 93    | 1.32 |
| <i>Amaurobius</i> sp.           | 2                | 0                | 2                | 4     | 0.10 | 0                | 0                | 0                | 0     |      |
| <i>Callioplus euoplus</i>       | 0                | 0                | 2                | 2     | 0.05 | 0                | 2                | 0                | 2     | 0.03 |
| <i>Callioplus tibialis</i>      | 0                | 18               | 22               | 40    | 1.00 | 2                | 25               | 10               | 37    | 0.52 |
| <i>Callioplus</i> sp.           | 1                | 0                | 0                | 1     | 0.02 | 0                | 2                | 1                | 3     | 0.04 |
| <i>Callobius bennetti</i>       | 20               | 57               | 67               | 144   | 3.58 | 42               | 113              | 40               | 195   | 2.75 |
| <i>Callobius</i> sp.            | 12               | 37               | 36               | 85    | 2.11 | 17               | 43               | 25               | 85    | 1.20 |
| Undet. sp.                      | 3                | 4                | 5                | 12    | 0.30 | 7                | 4                | 2                | 13    | 0.19 |
| DICTYNIDAE                      |                  |                  |                  |       |      |                  |                  |                  |       |      |
| <i>Dictyna brevitarsus</i>      | 1                | 0                | 0                | 1     | 0.02 | 0                | 0                | 0                | 0     |      |
| <i>Lathys pallida</i>           | 0                | 0                | 2                | 2     | 0.05 | 0                | 0                | 1                | 1     | 0.01 |
| Undet. sp.                      | 0                | 1                | 2                | 3     | 0.08 | 0                | 0                | 1                | 1     | 0.01 |
| THERIDIIDAE                     |                  |                  |                  |       |      |                  |                  |                  |       |      |
| <i>Robertus fuscus</i>          | 0                | 2                | 2                | 4     | 0.10 | 1                | 0                | 2                | 3     | 0.04 |
| <i>Robertus riparius</i>        | 17               | 2                | 11               | 30    | 0.75 | 14               | 6                | 5                | 25    | 0.36 |
| <i>Robertus</i> sp.             | 2                | 0                | 2                | 4     | 0.10 | 2                | 0                | 3                | 5     | 0.07 |
| <i>Theonoe stridula</i>         | 0                | 0                | 11               | 11    | 0.28 | 0                | 2                | 10               | 12    | 0.17 |
| <i>Theridion montanum</i>       | 0                | 0                | 0                | 0     |      | 0                | 2                | 0                | 2     | 0.03 |
| <i>Theridion sexpunctatum</i>   | 0                | 0                | 2                | 2     | 0.05 | 0                | 0                | 0                | 0     |      |
| <i>Theridion</i> sp.            | 0                | 0                | 2                | 2     | 0.05 | 0                | 0                | 2                | 2     | 0.03 |
| Undet. sp.                      | 1                | 0                | 1                | 2     | 0.05 | 0                | 0                | 0                | 0     |      |
| LINYPHIIDAE                     |                  |                  |                  |       |      |                  |                  |                  |       |      |
| <i>Agyneta olivacea</i>         | 0                | 0                | 0                | 0     |      | 0                | 1                | 1                | 2     | 0.03 |
| <i>Aphileta misera</i>          | 1                | 0                | 0                | 1     | 0.02 | 1                | 0                | 0                | 1     | 0.01 |
| <i>Bathypantes pallidus</i>     | 7                | 19               | 4                | 30    | 0.75 | 30               | 54               | 17               | 101   | 1.43 |
| <i>Bathypantes</i> sp.          | 1                | 0                | 1                | 2     | 0.05 | 0                | 0                | 0                | 0     |      |
| <i>Centromerus denticulatus</i> | 0                | 0                | 6                | 6     | 0.15 | 0                | 0                | 7                | 7     | 0.10 |

|  |    |    |    |     |      |    |    |     |     |      |
|--|----|----|----|-----|------|----|----|-----|-----|------|
| <i>Centromerus furcatus</i>                      | 4  | 11 | 16 | 31  | 0.78 | 4  | 8  | 7   | 19  | 0.27 |
| <i>Centromerus longibulbus</i>                   | 0  | 0  | 1  | 1   | 0.02 | 0  | 0  | 0   | 0   |      |
| <i>Centromerus persolutus</i>                    | 2  | 0  | 2  | 4   | 0.10 | 4  | 4  | 0   | 8   | 0.11 |
| <i>Lepthyphantes alpinus</i>                     | 0  | 16 | 19 | 35  | 0.88 | 3  | 37 | 50  | 90  | 1.27 |
| <i>Lepthyphantes complicatus</i>                 | 0  | 0  | 1  | 1   | 0.02 | 0  | 5  | 2   | 7   | 0.10 |
| <i>Lepthyphantes intricatus</i>                  | 2  | 13 | 3  | 18  | 0.45 | 6  | 14 | 4   | 24  | 0.34 |
| <i>Lepthyphantes</i> sp. near<br><i>arboreus</i> | 0  | 0  | 1  | 1   | 0.02 | 0  | 0  | 1   | 1   | 0.01 |
| <i>Lepthyphantes turbatrix</i>                   | 0  | 0  | 0  | 0   |      | 0  | 2  | 0   | 2   | 0.03 |
| <i>Lepthyphantes zebra</i>                       | 0  | 0  | 1  | 1   | 0.02 | 0  | 0  | 2   | 2   | 0.03 |
| <i>Lepthyphantes</i> sp.                         | 0  | 2  | 2  | 4   | 0.10 | 0  | 0  | 0   | 0   |      |
| <i>Meioneta simplex</i>                          | 0  | 0  | 0  | 0   |      | 4  | 0  | 0   | 4   | 0.06 |
| <i>Oreonetides flavescens</i>                    | 0  | 0  | 0  | 0   |      | 1  | 0  | 0   | 1   | 0.01 |
| <i>Oreonetides recurvatus</i>                    | 1  | 0  | 0  | 1   | 0.02 | 2  | 1  | 0   | 3   | 0.04 |
| <i>Oreonetides rotundus</i>                      | 0  | 2  | 0  | 2   | 0.05 | 1  | 0  | 1   | 2   | 0.03 |
| <i>Oreonetides vaginatus</i>                     | 0  | 10 | 22 | 32  | 0.80 | 4  | 19 | 14  | 37  | 0.52 |
| <i>Oreonetides</i> sp. 1                         | 0  | 0  | 0  | 0   |      | 0  | 0  | 2   | 2   | 0.03 |
| <i>Oreonetides</i> sp. 2                         | 2  | 1  | 1  | 4   | 0.10 | 3  | 11 | 2   | 16  | 0.23 |
| <i>Porrhomma</i> sp.                             | 1  | 1  | 0  | 2   | 0.05 | 0  | 1  | 1   | 2   | 0.03 |
| <i>Wubana drassoides</i>                         | 0  | 2  | 1  | 3   | 0.08 | 0  | 2  | 0   | 2   | 0.03 |
| Undet. sp.                                       | 2  | 1  | 1  | 4   | 0.10 | 10 | 18 | 24  | 52  | 0.74 |
| ERIGONIDAE                                       |    |    |    |     |      |    |    |     |     |      |
| <i>Baryphma longitarsum</i>                      | 1  | 0  | 0  | 1   | 0.02 | 3  | 0  | 0   | 3   | 0.04 |
| <i>Carorita limnaeus</i>                         | 0  | 0  | 0  | 0   |      | 0  | 0  | 2   | 2   | 0.03 |
| <i>Ceraticelus atriceps</i>                      | 1  | 0  | 0  | 1   | 0.02 | 0  | 0  | 0   | 0   |      |
| <i>Ceraticelus fissiceps</i>                     | 0  | 0  | 0  | 0   |      | 1  | 0  | 0   | 1   | 0.01 |
| <i>Ceraticelus laetabilis</i>                    | 5  | 6  | 1  | 12  | 0.30 | 21 | 16 | 3   | 40  | 0.57 |
| <i>Ceraticelus minutus</i>                       | 2  | 0  | 0  | 2   | 0.05 | 5  | 0  | 0   | 5   | 0.07 |
| <i>Ceratinella brunnea</i>                       | 13 | 5  | 34 | 52  | 1.30 | 32 | 81 | 83  | 196 | 2.77 |
| <i>Ceratinella</i> sp.                           | 9  | 2  | 2  | 13  | 0.33 | 6  | 5  | 6   | 17  | 0.24 |
| <i>Ceratinopsis auriculata</i>                   | 0  | 0  | 0  | 0   |      | 0  | 1  | 0   | 1   | 0.01 |
| <i>Dicymbium elongatum</i>                       | 0  | 0  | 0  | 0   |      | 1  | 0  | 1   | 2   | 0.03 |
| <i>Diplocentria bidentata</i>                    | 8  | 29 | 15 | 52  | 1.30 | 26 | 42 | 28  | 96  | 1.36 |
| <i>Diplocentria rectangulata</i>                 | 0  | 0  | 2  | 2   | 0.05 | 0  | 0  | 1   | 1   | 0.01 |
| <i>Diplocephalus cuneatus</i>                    | 1  | 0  | 1  | 2   | 0.05 | 0  | 0  | 0   | 0   |      |
| <i>Eperigone entomologica</i>                    | 0  | 0  | 0  | 0   |      | 0  | 4  | 3   | 7   | 0.10 |
| <i>Eperigone maculata</i>                        | 9  | 1  | 0  | 10  | 0.25 | 10 | 5  | 3   | 18  | 0.25 |
| <i>Eperigone trilobata</i>                       | 67 | 3  | 0  | 70  | 1.74 | 83 | 5  | 0   | 88  | 1.24 |
| <i>Erigone atra</i>                              | 1  | 1  | 0  | 2   | 0.05 | 0  | 0  | 0   | 0   |      |
| <i>Erigone</i> sp. 1                             | 1  | 0  | 0  | 1   | 0.02 | 0  | 0  | 0   | 0   |      |
| <i>Erigone</i> sp. 2                             | 1  | 0  | 0  | 1   | 0.02 | 0  | 0  | 0   | 0   |      |
| <i>Floricomus plumalis</i>                       | 3  | 0  | 3  | 6   | 0.15 | 9  | 1  | 3   | 13  | 0.19 |
| <i>Gnathonaroides pedale</i>                     | 0  | 0  | 0  | 0   |      | 0  | 0  | 1   | 1   | 0.01 |
| <i>Gonatium crassipalpus</i>                     | 0  | 1  | 0  | 1   | 0.02 | 0  | 0  | 0   | 0   |      |
| <i>Grammonota angusta</i>                        | 0  | 2  | 2  | 4   | 0.10 | 0  | 6  | 7   | 13  | 0.19 |
| <i>Grammonota gigas</i>                          | 0  | 0  | 0  | 0   |      | 12 | 1  | 0   | 13  | 0.19 |
| <i>Grammonota</i> sp.                            | 0  | 0  | 1  | 1   | 0.02 | 4  | 2  | 3   | 9   | 0.13 |
| <i>Halorates</i> sp.                             | 0  | 1  | 4  | 5   | 0.12 | 0  | 0  | 2   | 2   | 0.03 |
| <i>Islandiana longisetosa</i>                    | 0  | 0  | 0  | 0   |      | 0  | 1  | 0   | 1   | 0.01 |
| <i>Oedothorax trilobatus</i>                     | 2  | 0  | 0  | 2   | 0.05 | 1  | 0  | 0   | 1   | 0.01 |
| <i>Pocadicnemis americana</i>                    | 13 | 11 | 76 | 100 | 2.49 | 87 | 27 | 100 | 214 | 3.01 |
| <i>Sciasies truncatus</i>                        | 1  | 2  | 5  | 8   | 0.20 | 0  | 0  | 8   | 8   | 0.11 |
| <i>Scironis tarsalis</i>                         | 4  | 0  | 0  | 4   | 0.10 | 3  | 0  | 0   | 3   | 0.04 |
| <i>Scotinotylus pallidus</i>                     | 0  | 0  | 0  | 0   |      | 0  | 1  | 0   | 1   | 0.01 |
| <i>Sisicottus montanus</i>                       | 2  | 11 | 21 | 34  | 0.85 | 7  | 48 | 12  | 67  | 0.95 |
| <i>Sisicus apertus</i>                           | 0  | 0  | 1  | 1   | 0.02 | 0  | 0  | 0   | 0   |      |
| <i>Sisicus penifusiferus</i>                     | 0  | 0  | 1  | 1   | 0.02 | 0  | 0  | 0   | 0   |      |
| <i>Tapinocyba bicarinata</i>                     | 0  | 3  | 3  | 6   | 0.15 | 1  | 0  | 6   | 7   | 0.10 |



|                                  |      |     |    |      |       |      |     |    |      |       |
|----------------------------------|------|-----|----|------|-------|------|-----|----|------|-------|
| <i>Tapinocyba minuta</i>         | 0    | 1   | 1  | 2    | 0.05  | 7    | 6   | 1  | 14   | 0.20  |
| <i>Tapinocyba simplex</i>        | 0    | 3   | 13 | 16   | 0.40  | 6    | 14  | 15 | 35   | 0.49  |
| <i>Tunagyna debilis</i>          | 10   | 4   | 3  | 17   | 0.42  | 18   | 20  | 11 | 49   | 0.69  |
| <i>Walckenaeria atrotibialis</i> | 0    | 0   | 2  | 2    | 0.05  | 7    | 0   | 0  | 7    | 0.10  |
| <i>Walckenaeria castanea</i>     | 0    | 3   | 5  | 8    | 0.20  | 0    | 1   | 0  | 1    | 0.01  |
| <i>Walckenaeria communis</i>     | 0    | 0   | 0  | 0    |       | 1    | 0   | 1  | 2    | 0.03  |
| <i>Walckenaeria directa</i>      | 0    | 0   | 1  | 1    | 0.02  | 2    | 0   | 6  | 8    | 0.11  |
| <i>Walckenaeria exigua</i>       | 14   | 7   | 16 | 37   | 0.92  | 8    | 7   | 11 | 26   | 0.37  |
| <i>Walckenaeria spiralis</i>     | 1    | 0   | 0  | 1    | 0.02  | 4    | 0   | 0  | 4    | 0.06  |
| <i>Walckenaeria teres</i>        | 0    | 1   | 0  | 1    | 0.02  | 0    | 0   | 0  | 0    |       |
| Undet. sp.                       | 8    | 5   | 28 | 41   | 1.02  | 23   | 12  | 12 | 47   | 0.67  |
| <b>ARANEIDAE</b>                 |      |     |    |      |       |      |     |    |      |       |
| <i>Araneus nordmanni</i>         | 0    | 0   | 0  | 0    |       | 1    | 0   | 0  | 1    | 0.01  |
| Undet. sp.                       | 1    | 0   | 2  | 3    | 0.08  | 3    | 2   | 1  | 6    | 0.06  |
| <b>MIMETIDAE</b>                 |      |     |    |      |       |      |     |    |      |       |
| <i>Ero canionis</i>              | 1    | 0   | 1  | 2    | 0.05  | 0    | 0   | 1  | 1    | 0.01  |
| <i>Ero</i> sp.                   | 1    | 0   | 0  | 1    | 0.02  | 0    | 0   | 0  | 0    |       |
| <b>LYCOSIDAE</b>                 |      |     |    |      |       |      |     |    |      |       |
| <i>Alopecosa aculeata</i>        | 6    | 0   | 0  | 6    | 0.15  | 11   | 1   | 1  | 13   | 0.19  |
| <i>Alopecosa</i> sp.             | 0    | 0   | 4  | 4    | 0.10  | 0    | 0   | 0  | 0    |       |
| <i>Arctosa raptor</i>            | 1    | 0   | 0  | 1    | 0.02  | 0    | 0   | 0  | 0    |       |
| <i>Hogna</i> sp.                 | 2    | 0   | 0  | 2    | 0.05  | 0    | 0   | 0  | 0    |       |
| <i>Pardosa fuscula</i>           | 0    | 0   | 0  | 0    |       | 1    | 0   | 0  | 1    | 0.01  |
| <i>Pardosa hyperborea</i>        | 3    | 1   | 5  | 9    | 0.22  | 22   | 0   | 3  | 25   | 0.36  |
| <i>Pardosa mackenziana</i>       | 290  | 37  | 10 | 337  | 8.38  | 504  | 91  | 24 | 619  | 8.74  |
| <i>Pardosa maesta</i>            | 145  | 1   | 1  | 147  | 3.66  | 332  | 2   | 0  | 334  | 4.71  |
| <i>Pardosa xerampelina</i>       | 314  | 12  | 0  | 326  | 8.11  | 770  | 75  | 7  | 852  | 12.03 |
| <i>Pardosa</i> sp.               | 93   | 3   | 5  | 101  | 2.51  | 166  | 8   | 3  | 178  | 2.51  |
| <i>Pirata cantralli</i>          | 2    | 0   | 0  | 2    | 0.05  | 0    | 0   | 0  | 0    |       |
| <i>Pirata insularis</i>          | 6    | 0   | 9  | 15   | 0.37  | 7    | 0   | 4  | 11   | 0.16  |
| <i>Pirata minutus</i>            | 9    | 0   | 1  | 10   | 0.25  | 25   | 0   | 0  | 25   | 0.36  |
| <i>Pirata montanus</i>           | 0    | 0   | 0  | 0    |       | 2    | 0   | 1  | 3    | 0.04  |
| <i>Pirata piraticus</i>          | 4    | 1   | 0  | 5    | 0.12  | 1    | 0   | 0  | 1    | 0.01  |
| <i>Pirata</i> sp.                | 1    | 0   | 2  | 3    | 0.08  | 3    | 0   | 3  | 6    | 0.09  |
| <i>Trochosa terricola</i>        | 6    | 2   | 34 | 42   | 1.05  | 37   | 21  | 53 | 111  | 1.57  |
| <i>Trochosa</i> sp.              | 0    | 0   | 0  | 0    |       | 5    | 3   | 3  | 11   | 0.16  |
| Undet. sp.                       | 1133 | 113 | 2  | 1248 | 31.04 | 1368 | 222 | 56 | 1646 | 23.23 |
| <b>GNAPHOSIDAE</b>               |      |     |    |      |       |      |     |    |      |       |
| <i>Gnaphosa parvula</i>          | 2    | 0   | 0  | 2    | 0.05  | 7    | 0   | 0  | 7    | 0.10  |
| <i>Gnaphosa</i> sp.              | 0    | 0   | 0  | 0    |       | 1    | 0   | 0  | 1    | 0.01  |
| <i>Haplodrassus signifier</i>    | 1    | 0   | 0  | 1    | 0.02  | 2    | 0   | 1  | 3    | 0.04  |
| <i>Micaria pulcaria</i>          | 0    | 2   | 0  | 2    | 0.05  | 1    | 0   | 0  | 1    | 0.01  |
| <i>Orodassus canadensis</i>      | 0    | 1   | 0  | 1    | 0.02  | 0    | 0   | 0  | 0    |       |
| <i>Zelotes fratris</i>           | 9    | 0   | 2  | 11   | 0.28  | 27   | 0   | 2  | 29   | 0.41  |
| <i>Zelotes</i> sp.               | 2    | 0   | 0  | 2    | 0.05  | 18   | 1   | 0  | 19   | 0.27  |
| Undet. sp.                       | 1    | 0   | 0  | 1    | 0.02  | 1    | 0   | 0  | 1    | 0.01  |
| <b>CLUBIONIDAE</b>               |      |     |    |      |       |      |     |    |      |       |
| <i>Agroeca ornata</i>            | 0    | 1   | 8  | 9    | 0.22  | 1    | 6   | 11 | 18   | 0.25  |
| <i>Agroeca</i> sp.               | 0    | 0   | 2  | 2    | 0.05  | 0    | 0   | 1  | 1    | 0.01  |
| <i>Clubiona bishopi</i>          | 1    | 0   | 0  | 1    | 0.02  | 0    | 0   | 0  | 0    |       |
| <i>Clubiona canadensis</i>       | 0    | 5   | 8  | 13   | 0.33  | 0    | 8   | 2  | 10   | 0.14  |
| <i>Clubiona</i> sp.              | 3    | 0   | 1  | 4    | 0.10  | 0    | 7   | 2  | 9    | 0.13  |
| <b>PHILODROMIDAE</b>             |      |     |    |      |       |      |     |    |      |       |
| <i>Philodromus placidus</i>      | 1    | 1   | 1  | 3    | 0.08  | 1    | 2   | 1  | 4    | 0.06  |
| <i>Philodromus</i> sp.           | 0    | 0   | 0  | 0    |       | 0    | 1   | 1  | 2    | 0.03  |
| <i>Tibellus oblongus</i>         | 0    | 0   | 0  | 0    |       | 1    | 0   | 0  | 1    | 0.01  |
| <b>THOMISIDAE</b>                |      |     |    |      |       |      |     |    |      |       |
| <i>Ozyptila distans</i>          | 0    | 0   | 0  | 0    |       | 0    | 0   | 1  | 1    | 0.01  |
| <i>Xysticus canadensis</i>       | 0    | 19  | 35 | 54   | 1.34  | 2    | 88  | 95 | 185  | 2.61  |

|                                 |      |     |     |      |      |      |      |      |      |      |
|---------------------------------|------|-----|-----|------|------|------|------|------|------|------|
| <i>Xysticus discursans</i>      | 0    | 0   | 0   | 0    |      | 1    | 0    | 0    | 1    | 0.01 |
| <i>Xysticus emertoni</i>        | 0    | 0   | 0   | 0    |      | 7    | 0    | 0    | 7    | 0.10 |
| <i>Xysticus</i> sp.             | 0    | 0   | 2   | 2    | 0.05 | 0    | 2    | 2    | 4    | 0.06 |
| SALTICIDAE                      |      |     |     |      |      |      |      |      |      |      |
| <i>Euophrys cruciatus</i>       | 4    | 0   | 1   | 5    | 0.12 | 0    | 0    | 0    | 0    |      |
| <i>Evarcha hoyi</i>             | 0    | 0   | 0   | 0    |      | 2    | 0    | 0    | 2    | 0.03 |
| <i>Metaphidippus flavipedes</i> | 0    | 0   | 1   | 1    | 0.02 | 0    | 1    | 2    | 3    | 0.04 |
| <i>Pellenes montanus</i>        | 0    | 0   | 0   | 0    |      | 4    | 0    | 0    | 4    | 0.06 |
| <i>Phidippus borealis</i>       | 0    | 0   | 0   | 0    |      | 3    | 0    | 0    | 3    | 0.04 |
| <i>Phidippus whitemanii</i>     | 0    | 0   | 0   | 0    |      | 1    | 0    | 0    | 1    | 0.01 |
| <i>Sitticus finschii</i>        | 0    | 0   | 1   | 1    | 0.02 | 0    | 0    | 0    | 0    |      |
| Undet. sp.                      | 0    | 0   | 0   | 0    |      | 0    | 0    | 1    | 1    | 0.01 |
| UNIDENTIFIABLE                  | 0    | 0   | 0   | 0    |      | 1    | 0    | 0    | 1    | 0.01 |
| Subtotals:                      |      |     |     |      |      |      |      |      |      |      |
| Species                         | 59   | 51  | 68  |      |      | 76   | 56   | 69   |      |      |
| Individuals                     | 2412 | 639 | 971 | 4022 |      | 4340 | 1627 | 1118 | 7085 |      |

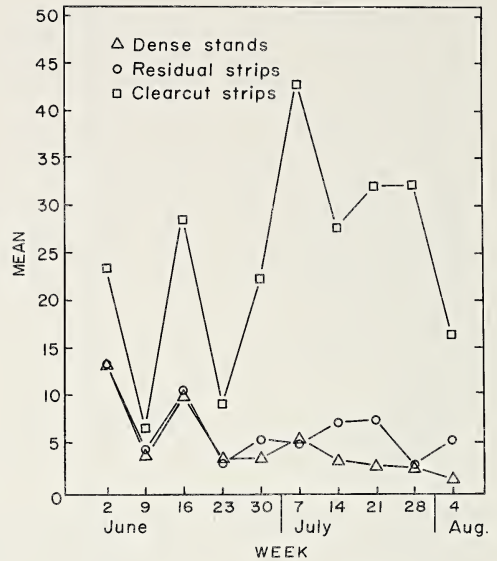
Species of spiders that showed habitat affinities both study years were: *Neoantistea magna* (Keyserling), *Eperigone trilobata* (Emerton), *Pardosa mackenziana* (Keyserling), *P. moesta* Banks, *P. xerampelina* (Keyserling), *Pirata minutus* Emerton, and *Zelotes fratris* Chamberlin for clearcut strips; *Bathypantes pallidus* (Banks) and *Diplocentria bidentata* (Emerton) for uncut residual strips; *Wadotes calcaratus* (Keyserling), *Callobius bennetti* (Blackwall), *Lepthyphantes alpinus* (Emerton), *Oreonetides vaginatus* (Thorell), *Ceratinella brunnea* Emerton, *Sisicottus montanus* (Emerton), and *Xysticus canadensis* Gertsch for uncut residual strips, dense stands, or both uncut forest conditions. Habitat preferences of *Pocadicnemis americana* Millidge and *Trochosa terricola* Thorell were undeterminable from our data. In 1977 and 1978, both species were most abundant in dense stands; however, in 1978, both species were also prevalent in clearcut strips. Pitfall catches for the remaining species showed no clear habitat preference or affinity.

**Mean numbers of individuals and species.**—For both study years, significantly more individuals (ANOVA,  $F = 84.7$ ,  $P \leq 0.0001$ , 1977;  $F = 41.7$ ,  $P \leq 0.0001$ , 1978) and more species (ANOVA,  $F = 32.3$ ,  $P \leq 0.0001$ , 1977;  $F = 13.4$ ,  $P \leq 0.0001$ , 1978) of spiders were captured in clearcut strips than in either uncut residual strips or dense stands (Table 2). And, for both study years, the most similar habitats (i.e., uncut residual strips and dense stands) did not differ significantly for mean numbers of individuals per trap per week. Likewise, mean numbers of species did not differ significantly either study year.

Table 2.—Mean numbers of individuals and spider species per trap per week by forest condition. Column means followed by the same letter are not significantly different at the  $P \leq 0.05$  level, Duncan's multiple range test. Natural log transformations,  $\ln(x + 1)$ , were used to stabilize variances of mean numbers of individuals.

| Forest condition | $\bar{X} (\pm SE)$ individuals |               | $\bar{X} (\pm SE)$ species |              |
|------------------|--------------------------------|---------------|----------------------------|--------------|
|                  | 1977                           | 1978          | 1977                       | 1978         |
| Clearcut strips  | 24.12a (2.21)                  | 28.18a (2.04) | 5.98a (0.27)               | 7.40a (0.35) |
| Residual strips  | 6.39b (0.70)                   | 10.56b (0.80) | 3.94b (0.29)               | 5.77b (0.31) |
| Dense stands     | 4.85b (0.33)                   | 8.48b (0.64)  | 3.33b (0.19)               | 5.06b (0.32) |

Fig. 2.—Mean catches of spiders per trap per week; week 1 = 2 June 1977. Open triangles = dense spruce-fir stands; open circles = uncut residual strips; open squares = clearcut strips.



**Seasonal activity.**—Spiders were active during most of the spruce budworm's developmental stages; however, seasonal activities varied between study years and among forest conditions (Figs. 2 and 3). For both study years, mean catch densities per week were greater in clearcut strips; whereas, mean catches were about equal for uncut residual strips and dense stands. In both 1977 and 1978, peak catches were observed the 3rd and 6th weeks for clearcut strips; the latter peaks generally corresponded with emergence of young spiderlings. Mean catches of individuals per week generally declined about the 3rd (1977) and 2nd (1978) weeks of trapping for both dense stands and uncut residual strips.

Mean species per trap also fluctuated between years and among forest conditions (Figs. 4 and 5). Strip clearcuts generally had more species per trap per week than the other two forest conditions. For both study years, mean species catch rate generally declined after the 5th and 6th weeks of trapping; however, in 1978 catch rates increased during the 10th and 11th weeks.

**Species diversity and evenness.**—Although more individuals and species of spiders were captured in clearcut strips, species diversity and evenness of pitfall-trap catches were generally greater in dense stands and uncut residual strips (Table 3). The most similar habitats (i.e., uncut residual strips and dense stands) had comparable diversity and evenness values both years. No doubt the uneven distribution of individuals in clearcut strips contributed to lower species diversity for these habitats. Species diversity increases as individuals become more evenly distributed (Price 1975). The higher observed variances in mean individuals per trap per week (Table 2) also indicate unevenly distributed individuals for clearcut-strip habitats.

**Coefficient of community and percentage similarity.**—Strip-clearcut areas (uncut residual and clearcut strips) and dense stands shared about the same number of species of spiders either study year; CC = 68.1 in 1977; CC = 66.2 in 1978. Surprisingly, the most dissimilar neighboring habitats (i.e., uncut residual and clearcut strips) had only slightly fewer species in common; CC = 58.7 in 1977; CC = 62.1 in 1978.



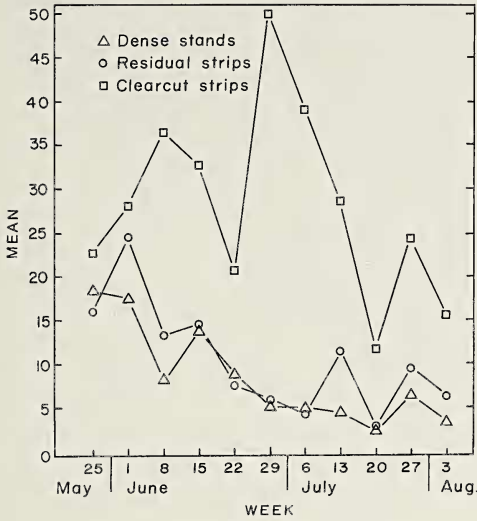


Fig. 3.—Mean catches of spiders per trap per week; week 1 = 25 May 1978. Open triangles = dense spruce-fir stands; open circles = uncut residual strips; open squares = clearcut strips.

Among strip-clearcut areas and dense stands, percentage similarity in numbers of individuals of each spider species was about the same both study years, i.e.,  $PS = 39.6$  in 1977;  $PS = 39.9$  in 1978. However, comparing catches *within* strip clearcuts (uncut residual vs. clearcut strips) showed that fewer individuals shared these habitats in common in 1977 ( $PS = 22.8$ ) than in 1978 ( $PS = 32.8$ ). The relatively low  $PS$  values support our hypothesis that the unevenly distributed individuals in clearcut strips contributed greatly to lower species diversity for these habitats.

**Age of strip clearcut.**—Regression analyses indicated that age of strip clearcut (1-6 years) had little influence on mean catches of individuals ( $R^2 = 0.08$ ,  $P > 0.37$ ) and mean numbers of species ( $R^2 = 0.41$ ,  $P > 0.02$ ) of spiders/trap/week.

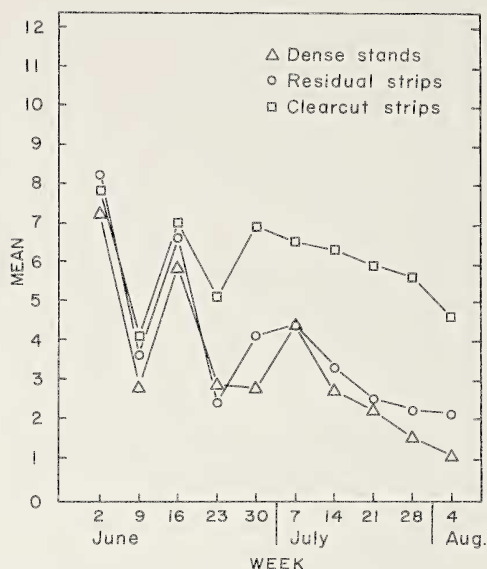
**Litter depth.**—Mean litter depth was significantly greater ( $P \leq 0.01$ ) in dense stands ( $\bar{X} = 11.7$  cm) than in either uncut residual ( $\bar{X} = 8.5$  cm) or in clearcut strips ( $\bar{X} = 8.0$  cm). Uncut residual and clearcut-strip means did not differ significantly. Regression analyses indicated that litter depth had little influence on either mean catches ( $R^2 = 0.04$ ,  $P \geq 0.08$ ) or mean species ( $R^2 = 0.05$ ,  $P \geq 0.05$ ) of spiders/trap/week.

## DISCUSSION

Few previous studies have dealt with Maine spiders. The spider fauna of Mount Desert Island, Hancock County, has been studied most extensively; Procter (1946) listed 15 families, 94 genera, and 179 species from various habitats on the island. Earlier, Bishop and Clarke (1923) reported spiders of 10 families, 23 genera, and 29 species from Isle au Haut, Knox County, Maine. Blake (1926) studied the biota of Mount Katahdin, Piscataquis County, and reported the collection of 20 species, which represent 14 genera and 11 families of spiders. Mount Katahdin is about 25 km southeast of our spruce-fir study area. Our collections of spiders from spruce-fir forests in Piscataquis County substantially adds to the species recorded from Maine.

Our results on mean catches of individuals and species per trap per week generally indicate that the ground-inhabiting spiders preferred the more open,

Fig. 4.—Mean species of spiders per trap per week; week 1 = 2 June 1977. Open triangles = dense spruce-fir stands; open circles = uncut residual strips; open squares = clearcut strips.



cleared habitats of clearcut strips to that of closed, shaded habitats of uncut residual strips and dense stands. Significantly more individuals and species were caught in the clearcut strips both study years (Table 2). However, most of this unequal distribution can be attributed to the greater abundance of lycosid spiders, and particularly *Pardosa* species, in the clearcut strips. For both study years, significantly more ( $P \leq 0.05$ ) individuals of *Pardosa* species were trapped in the clearcut strips than in the other forest conditions,  $\bar{X} = 8.4/\text{trap}/\text{week}$  in 1977 and  $\bar{X} = 11.7/\text{trap}/\text{week}$  in 1978.

Measures of similarity among forest conditions indicated that more species (CC values) than individuals (PS values) shared forest conditions in common. No doubt heterogeneity of habitats and individual species requirements influenced the species composition and spatial distributions of spiders among the forest conditions studied. Species such as *Neoantistea magna*, *Pardosa mackenziana*, and *P. xerampelina* showed definite habitat affinities for clearcut strips; other species, such as *Wadotes calcaratus*, *Callobius bennetti*, *Lepthyphantes alpinus*, and *Xysticus canadensis* were intermediate in habitat association (i.e., two forest conditions, both similar); whereas, *Pocadicnemis americana* and *Trochosa terricola* were indeterminate regarding habitat preference.

Because species diversity and evenness of pitfall trap-catches were generally lower in clearcut strips both study years, we conclude that strip clearcutting may alter species richness and abundance of ground-dwelling spiders in northeastern spruce-fir forests. The open, cleared strips with abundant shrubs and forbs provide new and different habitats where hunting spiders (e.g., Lycosidae) abound. Coyle (1981) also found an abundance of hunting spiders in clearcuts of a southern Appalachian forest. The uncut residual stands of northern Maine, conversely, provide islands of "refugia" where spider populations are diverse. Thus, the overall effect of strip clearcutting (clearcut and uncut residual strips) is a reduction in species diversity and evenness of spiders (Table 3), but an increase in spider abundance (Table 2). With time and plant succession, the strip-clearcut areas should provide macrohabitats and microhabitats similar to dense stands.

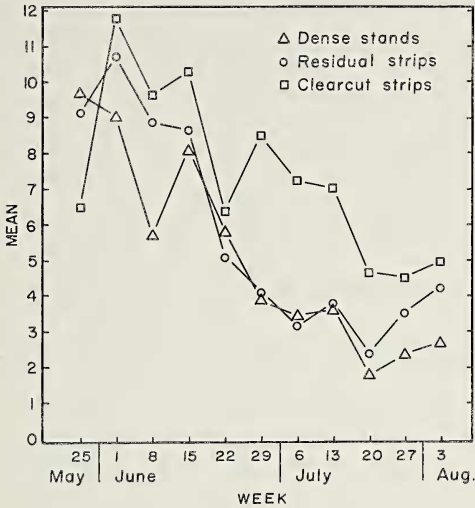


Fig. 5.—Mean species of spiders per trap per week; week 1 = 25 May 1978. Open triangles = dense spruce-fir stands; open circles = uncut residual strips; open squares = clearcut strips.

We detected little influence of either strip-clearcut age or litter depth on mean overall catches of individuals and species of spiders. However, strip-clearcut age may become increasingly important during later successional stages when forest regeneration causes canopy closure. Canopy closure, or absence thereof, apparently had a dramatic effect on the abundance and distribution of certain Lycosidae (e.g., species of *Pardosa*) in the northeastern spruce-fir forest. Most of the wolf spiders were found in open, sunny areas of clearcut strips, with lesser numbers in closed, shaded areas of dense stands and uncut residual strips. Bultman et al. (1982) also found a scarcity of wolf spiders in a beech-maple climax forest of western Michigan.

Several investigators (Hagstrum 1970; Uetz 1979; Bultman et al. 1982) have concluded that litter depth is an important factor that influences spider abundance, particularly in deciduous forests. We suspect that litter depth may have lesser influence on spider abundance in coniferous forests where litter structure tends to be fairly uniform. Absence of canopy closure probably has a more significant effect on overall spider abundance in spruce-fir forests, and particularly on the abundance of *Pardosa* species. Our results on species diversity (Table 3) and litter depth generally agree with Uetz (1979); i.e., species diversity increased with increased litter depth of uncut dense stands.

Based on pitfall-catch densities, spiders were abundant and active during the spruce budworm's early and late larval stages, and during budworm oviposition and dispersal of first instars (weeks 8-10). Spruce budworm oviposition generally spans 27 days in late June and July (Houseweart et al. 1982), and budworm eggs are susceptible to predation by arboreal spiders (Jennings and Houseweart 1978). After budworm eggs hatch (ca. 10 days), the young larvae disperse and seek overwintering sites. However, during dispersal many budworms are lost because the larvae land on nonhost vegetation (Morris and Mott 1963); they also are susceptible to predation by spiders (Mott 1963). Strip-clearcutting contributed to dispersal losses of early-instar budworms (Jennings et al. 1983). Results of the current study indicate that budworm larve landing in clearcut strips would be especially susceptible to attack by lycosid spiders because of the latter's great abundance. Predation on dropping late-instar budworms may also be significant



Table 3.—Spider species diversity and evenness of pitfall-trap catches by forest condition, Brillouin's formula, 1977 and 1978. 1977, 5 replicates each forest condition; 4 traps/replicate. 1978, 7 replicates (residual vs. clearcut strips); 3 replicates (residual + clearcut strips vs. dense stands); 4 traps/replicate.

| Forest condition           | Diversity |      | Evenness |      |
|----------------------------|-----------|------|----------|------|
|                            | 1977      | 1978 | 1977     | 1978 |
| Residual strips            | 1.31      | 1.37 | 0.81     | 0.81 |
| Clearcut strips            | 0.98      | 1.08 | 0.57     | 0.58 |
| Residual + clearcut strips | 1.23      | 1.14 | 0.67     | 0.63 |
| Dense stands               | 1.33      | 1.36 | 0.76     | 0.77 |

because mortality during the late larval stage influences generation survival of the spruce budworm (Morris 1963).

Additional studies are needed to determine the predatory roles of spiders in northeastern spruce-fir forests and their impacts on spruce budworm populations. Such studies will require assessment of both predator and prey densities, and specialized techniques, such as the ELISA assay (Fichter and Stephen 1979; Ragsdale et al. 1981), to determine numbers of spruce budworms eaten by spiders.

Enhancement of predator populations through forest management procedures is receiving increased attention (Crawford and Titterington 1979; Jennings and Crawford 1985). The current study indicates that populations of ground-dwelling spiders can be greatly increased by strip clearcutting; however, the long-term effects of strip clearcutting on changes in spider species diversity are unknown. Much more information is needed to develop sound, realistic pest management systems that promote and utilize natural agents of mortality and rely less on chemical insecticides.

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